

# Taxonomic reexamination of three vesicomimid species (Bivalvia) from the middle Miocene Bessho Formation in Nagano Prefecture, central Japan, with notes on vesicomimid diversity

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## ABSTRACT

The middle Miocene Bessho Formation in central Japan consists of siltstone deposited on the slope of a back-arc basin, and contains cold-seep carbonate bodies of various sizes. We describe four vesicomimid species from this formation, one of them new, *Pliocardia?* *tanakai* new species, one in open nomenclature, *Adulomya* sp. 1, and two previously reported species, *Adulomya uchimuraensis* Kuroda, 1931 and *Calyptogena akanudaensis* Tanaka, 1959, the latter here reassigned to the genus *Adulomya*. The relative abundances of the four vesicomimid species are different among fossil localities, apparently related to size, lithology, and the carbon isotopic signature of the carbonate bodies. First, large carbonate mounds composed of micrite and calcite veins, with  $\delta^{13}\text{C}$  values of  $-40$  to  $-36\text{‰}$  vs. PDB, are dominated by *A. uchimuraensis*, with *A. akanudaensis* and *Pliocardia?* *tanakai* new species being minor constituents. Second, siltstone containing em-sized carbonate concretions with  $\delta^{13}\text{C}$  values as low as  $-35\text{‰}$  contains only rare and scattered specimens of *Adulomya* sp. 1. Third, at a carbonate body,  $\sim 1$  m in diameter and composed mainly of micrite with  $\delta^{13}\text{C}$  values of  $-29.8$  to  $+10.5\text{‰}$ , *A. akanudaensis* and *A. uchimuraensis* are about equally abundant. These distribution patterns suggest that the vesicomimid species diversity in the Bessho Formation might have been related to variations in the physico-chemical characteristics of the seep environment, such as fluid flux rates and/or seep longevity.

*Additional Keywords:* *Pliocardia*, new species, *Adulomya*, Vesicomimidae, middle Miocene, cold seeps

## INTRODUCTION

Vesicomimid bivalves first appeared at the middle Eocene cold-seep sites in North Pacific, and they are now dominant animals in various deep-sea reducing environments such as cold seeps, hydrothermal vents, and whale falls all over the world (Amano and Kiel, 2007; Taylor and Glover, 2010; Krylova and Sahling, 2010). The family

Vesicomimidae is one of the most species-rich families among chemosynthesis-based animals, with more than 100 species described so far (Decker et al., 2012). A recent molecular phylogenetic analysis of the vesicomimids by Decker et al. (2012) suggested recurrent events of “stepwise speciation” from shallow to deep waters in different ocean basins, which is consistent with bathymetric segregation among the extant genera and species (Fujikura et al., 2000; Cosel and Olu, 2009; Krylova and Sahling, 2010). For more discussion on vesicomimid species diversity we should also pay attention to co-occurrences of two or more species from the same area, both in modern (e.g., Callender and Powell, 1992; Barry et al., 1997; Kojima and Ohta, 1997; Krylova and Janssen, 2006; Fujikura et al., 2008) and ancient seep sites (Tanaka, 1959; Amano et al., 2010; Kiel, 2010; Kiel and Amano, 2010; Amano and Kiel, 2012).

The middle Miocene Bessho Formation in Nagano Prefecture, central Japan, hosts cold-seep carbonate bodies of various sizes, some of which yield two or more vesicomimid species (Koike and Miyajima, 2016). The large seep carbonate bodies at Akanuda and Anazawa have been reported to yield two vesicomimid species, *Adulomya uchimuraensis* Kuroda, 1931, and *Calyptogena akanudaensis* Tanaka, 1959 (Tanaka, 1959; Kanno et al., 1998). *Adulomya uchimuraensis* has been studied and revised by Kanno et al. (1998) and Amano and Kiel (2011), but *C. akanudaensis* was beyond the scope of these studies and its generic assignment was postponed, because its internal characters were unknown.

This paper focuses on taxonomical reexamination on vesicomimid species from the Bessho Formation. We reassign *Calyptogena akanudaensis* to the genus *Adulomya* Kuroda, 1931, on the basis of its internal shell characters recognized in type materials and our newly collected fossil specimens. We also newly describe *Pliocardia?* *tanakai* new species and report another species, *Adulomya* sp. 1, in open nomenclature. Habitat preferences of the four species are discussed based on their relative abundance,

mode of occurrences, and the petrographic and geochemical characteristics of the hosting seep carbonates.

## MATERIALS AND METHODS

The Bessho Formation is mainly composed of dark-gray siltstone deposited at a back-arc basin after the opening of the Japan Sea (Harayama, 2006). The examined vesicomid fossils are from three localities in the northern part of Matsumoto City, i.e., Akanuda and Anazawa (Loc. 1), Sorimachi (Loc. 2), and Tonohara (Loc. 3), as shown in Figure 1. Kato et al. (2011) estimated the sedimentary environment of the Bessho Formation to be upper- to upper middle-bathyal depths under warm current, based on a benthic foraminiferal assemblage from Loc. 1 and other fossil occurrences (Kosaka and Taguchi, 1983; Noda et al., 1986; Itoigawa and Yanagisawa, 2002). Kato et al. (2011) assigned the planktonic foraminiferal and calcareous nannofossil assemblages from Loc. 1 to the PF2/PF3 zones of Maiya (1978) and the CN5a zone of Okada and Burkry (1980), corresponding to an absolute age of 13.6 to 13.1 Ma, according to Saito (1999).

We reexamined vesicomid fossil specimens in the collection of Kunio Tanaka (Emeritus Professor of Shinshu University, Japan) from seep carbonate bodies at Akanuda and Tonohara (Locs. 1 and 3), which are deposited in the Shinshushinmachi Fossil Museum (SFMKT-00144, 00389, 00398, 00399, 00401–00407, and 07227–07230). In addition, abundant vesicomid fossil specimens collected by us from the three localities were also examined. The specimens were carefully cleaned

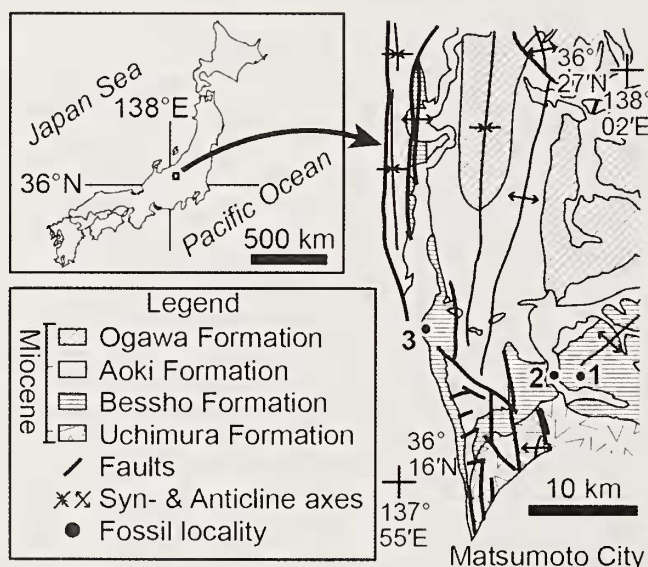
using an air scribe and needles to expose hinge characters, measured to the nearest 0.1 mm using a caliper, and photographed with ammonium chloride coating. All specimens are deposited in the Shinshushinmachi Fossil Museum (SFM) and the Department of Geology and Mineralogy, Kyoto University, Japan (KUG).

We analyzed carbon stable isotopic compositions of the carbonates from localities 2 and 3, in order to examine whether or not they were related to methane seepage. Powdered samples, taken from cut slabs using a micro-drill, were reacted with 100% orthophosphoric acid in vacuum at 90 °C for 1000 s, and analyzed in a mass spectrometer IsoPrime 100 (Isoprime) at the Department of Geology and Mineralogy, Kyoto University. Isotope values are expressed as a per-mil difference between the sample and the PDB standard in delta notation. External precision for the standard material was better than 0.1‰.

## LITHOLOGY AND MODE OF FOSSIL OCCURRENCE

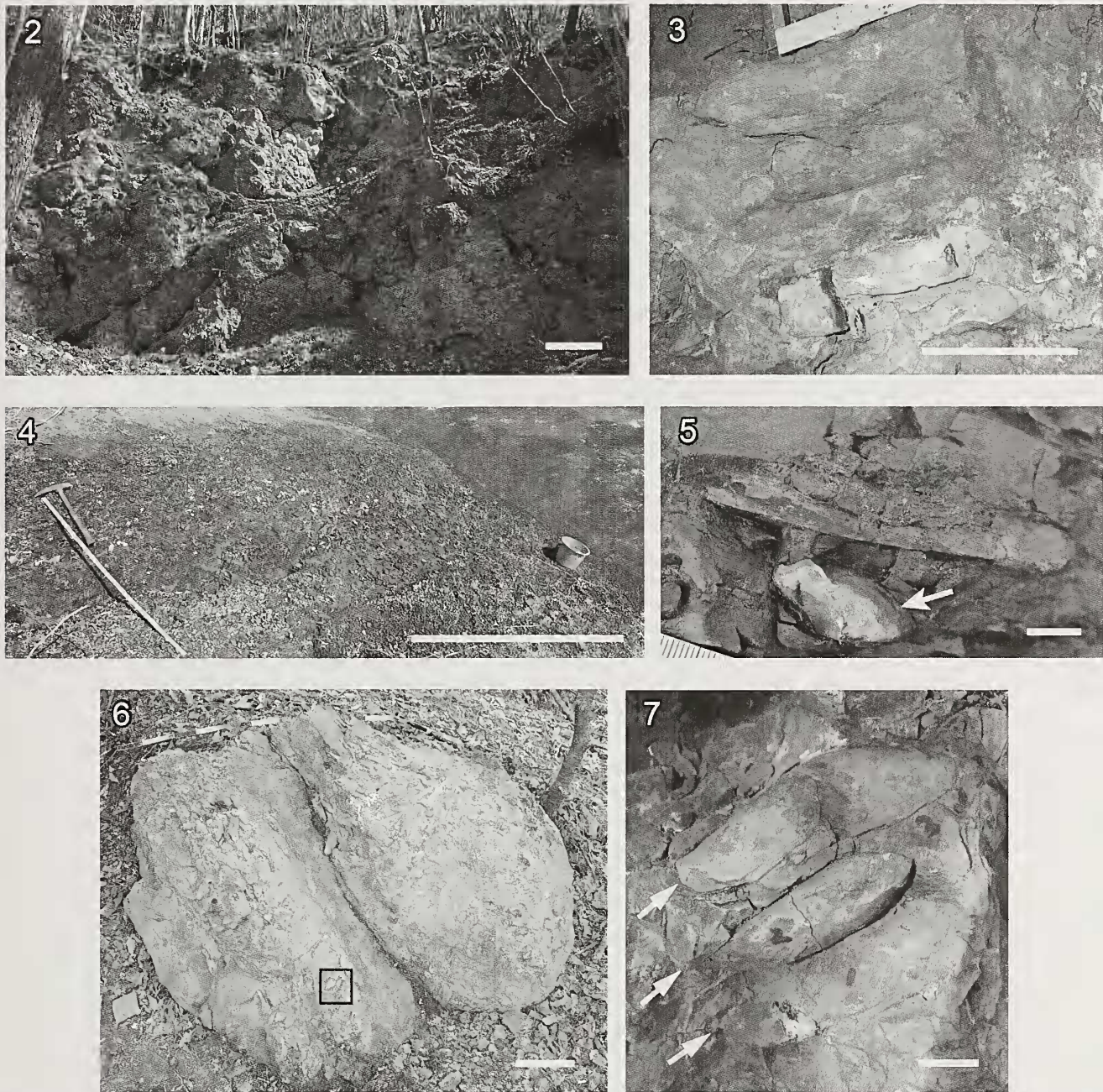
Seep carbonate size, lithology, and mode of fossil occurrence differ among the studied localities. At Akanuda and Anazawa (Loc. 1), large-sized seep-carbonate mounds, up to 20 m in diameter, are intercalated within the dark-gray massive siltstone (Figure 2). The carbonate mounds consist of muddy micrite with sparitic veins and veinlets, both showing low  $\delta^{13}\text{C}$  values (−40 to −36‰ vs. PDB; Sato et al., 1993) originating from the anaerobic oxidation of methane (Peckmann and Thiel, 2004). These seep carbonates yield abundant molluscan fossils dominated by a large and elongate vesicomid, *Adulomya uchimuraensis*, with patchy clusters of a bathymodiolin mussel, “*Bathymodiolus*” *akanudaensis* (Tanaka, 1959; Kanno et al., 1998; Nobuhara et al., 2008; Nobuhara, 2010). In addition, the fossil fauna of the seep carbonates at this locality is characterized by a high species diversity, including bivalves *Conchocelea bisecta* (Conrad, 1849), *Lucinoma* sp., and *Megathracia* sp., and gastropods *Provanna* sp., *Margarites* sp., *Comitas* sp., and *Trophonopsis* sp. The vesicomid *A. uchimuraensis* and “*B.*” *akanudaensis* often form shell clusters composed of conjoined valves, indicating *in-situ* burial of the colonies (Figure 3). Tanaka (1959) described *Calypptogena akanudaensis* from Akanuda, but we failed to collect new specimens of this species from this locality, suggesting that it is a rare species. Tanaka (1959) also reported the bivalves *Paphia* sp. and *Liocyma* cf. *terrera* from Akanuda, both of which are here redescribed as a new vesicomid species, *Pliocardia?* *tanakai* new species. We found seven additional specimens of this species, three of which were collected from the marginal part of the carbonate mound at Anazawa.

At Sorimachi (Loc. 2), located about 1.3 to 1.5 km west of Loc. 1, dark-gray siltstone containing small carbonate concretions, several centimeters in diameter, is exposed on a riverside cliff of the Hofukuji River (Figure 4). The carbonate concretions show  $\delta^{13}\text{C}$  values as low as −35‰,



**Figure 1.** The geological map of the northern area of Matsumoto City, Nagano Prefecture (modified from Seki, 1983; Yamada et al., 1989; Nakano et al., 1998; Harayama et al., 2009) showing the localities of the vesicomid fossils described herein. 1: Anazawa and Akanuda limestones. 2: Sorimachi. 3: Tonohara.





**Figures 2–7.** Study outcrops. **2.** Large seep carbonate body at Anazawa, Loc. 1. Scale bar = 1 m. **3.** Cluster of articulated valves of *Adulomya uchimuraensis* Kuroda in the carbonate body at Loc. 1. Scale Bar = 0.1 m. **4.** Siltstone containing abundant small carbonate concretions at Sorimachi, Loc. 2. Scale bar = 1 m. **5.** Single articulated valves of *Adulomya* sp. 1 contained in the siltstone at Loc. 2. White arrow points a carbonate concretion. Scale bar = 10 mm. **6.** Carbonate block at Tonohara, Loc. 3. Square indicates three fossils of *A. akanudaensis* enlarged in **7**. Scale bar = 0.2 m. **7.** Cluster of three articulated valves of *A. akanudaensis* (Tanaka) contained in the carbonate block at Loc. 3. White arrows indicate each fossil and its anterior direction. Note that all valves are arranged in parallel with their anterior sides in similar directions. Scale bar = 10 mm.

suggesting methane seepage at this site (details will be reported elsewhere). Mostly conjoined shells of small and elongated vesicomid fossils are scattered throughout the siltstone, with their commissure planes parallel to the bedding plane (Figure 5). The species composition at Loc. 2 is monotonous and consists mainly of this

vesicomid, with rare lucinid and solemyid bivalves. Although the vesicomid fossils from this locality were once identified as *Adulomya uchimuraensis* by Tanaka (1960) and Seki (1983), we show that they are distinguishable from *A. uchimuraensis* and report them in open nomenclature, as *Adulomya* sp. 1.



At Tonohara (Loc. 3), a carbonate body of ~1.1 m diameter is exposed on a slope (Figure 6). This carbonate body is entirely micritic, lacks sparitic cement, and has  $\delta^{13}\text{C}$  values ranging from  $-29.8$  to  $+10.5\%$ . Those parts of the carbonate body having positive  $\delta^{13}\text{C}$  values could have originated from the  $^{13}\text{C}$ -enriched  $\text{CO}_2$  pool in the methanogenesis zone (Irwin et al., 1977), whereas those parts showing negative and low  $\delta^{13}\text{C}$  values could have formed via the anaerobic oxidation of methane, suggesting that this locality was affected by methane seepage. This carbonate body contains *Adulomya uchimuraensis*, “*Calypptogena*” *akanudaensis*, *Conchocele* sp., and gastropod fossils. The species composition is similar to that of the large carbonate mounds at Akanuda and Anazawa (Loc. 1), but it differs from the latter in 1) “*C.*” *akanudaensis* and *A. uchimuraensis* being about equally abundant, and 2) having a lower species diversity lacking *Bathymodiolus*, *Pliocardia*, and *Provanna*. Most bivalve fossils are conjoined and often found in *in-situ* burial mode, in which all valves are arranged in parallel with their anterior sides in similar directions (Figure 7).

#### SYSTEMATIC PALEONTOLOGY

Family Vesicomylidae Dall and Simpson, 1901  
Subfamily Pliocardiinae Woodring, 1925

#### Genus *Pliocardia* Woodring, 1925

**Type Species:** *Anomalocardia bowdeniana* Dall, 1903 from the upper Pliocene Bowden Formation in Jamaica (original designation).

**Remarks:** Krylova and Janssen (2006) redefined the genus *Pliocardia* as small- to medium-sized elliptical vesicomylid characterized by a shallow radial depression from umbo to postero-ventral margin, a deep lunular incision, a shallow pallial sinus, and a stout ventral tooth (1) overlying the subumbonal cardinals (3a, 3b) in the right valve. *Pliocardia* is similar to *Vesicomya* in its small shell size, clearly incised lunule, and dentition (Woodring, 1925), but differs from the latter by having thicker shells and a much thicker posterior cardinal tooth (Amano and Kiel, 2007). *Pliocardia* is also similar to *Archivesica* Dall, 1908 in dentition, but distinguished from the latter by having a much smaller shell and an escutcheon, and lacking a subumbonal pit (Amano and Kiel, 2007, 2010; Krylova et al., 2014).

Recently, Martin and Goffredi (2012) acknowledged a need for a taxonomic revision of *Pliocardia*. They newly described “*Pliocardia*” *krylovata* from the Costa Rica Margin based on molecular evidence. “*Pliocardia*” *krylovata* has a thick shell, a shallow postero-ventral depression, a shallow lunular incision, a shallow but complex pallial sinus, and a remarkably deep escutcheon. The latter two characters have not yet been recognized in *Pliocardia* (sensu stricto).

#### *Pliocardia?* *tanakai* new species

(Figures 8–23)

*Liocyma* cf. *terrera* (Yokoyama).—Tanaka, 1959: 121–122, pl. 3, figs. 21–22.

*Paphia* sp. Tanaka, 1959: 122, pl. 3, fig. 23.

**Diagnosis:** Small-sized ovate vesicomylid with pointed posterior end in adult, well-defined lunular incision, ventral cardinal tooth (1) thick and anterior cardinal tooth (3a) very short in right valve hinge, anterior cardinal tooth (2a) thin and middle cardinal tooth (2b) knob-shaped, both connected at nearly right angle in their proximal parts just below umbo in left valve hinge, a blunt ridge from umbo to postero-ventral corner on internal surface but no radial depression on external surface which corresponds to the internal blunt ridge, pallial sinus lacking.

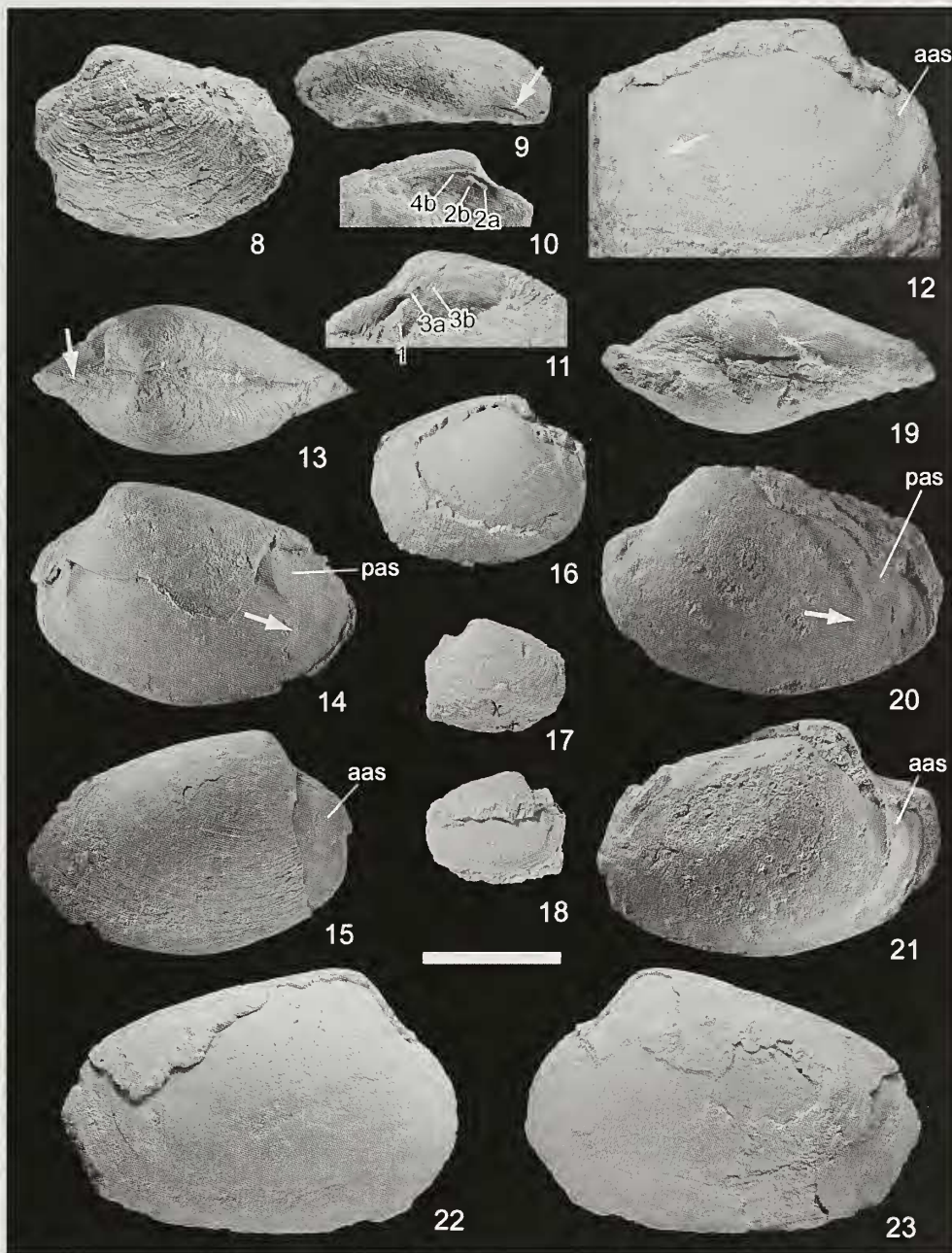
**Description:** Shell thin, small in size (up to 28.4 mm in length), ovate in outline (height/length = 0.57–0.78), more rounded in juvenile (length < 16 mm), equivalve and inequilateral, moderately inflated (width/length = 0.28–0.55), ornamented with fine commarginal growth lines. Antero-dorsal margin slightly concave, continuing to rounded and slightly convex anterior margin; postero-dorsal margin nearly straight, obtusely angulate at transition to posterior margin; posterior margin rounded in juvenile but more pointed with growth; ventral margin broadly arcuate. Beak prominent, prosogyrate and located at 26–38% of shell length from anterior end. Lunule well defined by distinct lunular incision. Escutcheon narrow and shallowly depressed. Right valve hinge: ventral cardinal tooth (1) moderately thick, subparallel to antero-dorsal shell margin, overlain by anterior cardinal tooth (3a) in its posterior end; anterior cardinal (3a) very short, parallel to shell margin; entire shape of posterior cardinal (3b) unclear due to recrystallization of the shell. Left valve hinge: anterior cardinal (2a) thin, parallel to antero-dorsal shell margin; middle cardinal (2b) short and knob-shaped, situated just below umbo, connected with anterior cardinal (2a) at nearly right angle in their proximal parts; posterior cardinal (4b) slightly thinner but as long as anterior cardinal (2a), subparallel to postero-dorsal shell margin, detached from other cardinals (2a and 2b). Anterior adductor muscle scar ovate with rather straight and deeply impressed posterior margin. Posterior adductor muscle scar ovate with deeply impressed anterior margin forming a blunt inner ridge running from beak. Pallial line entire, starting at postero-ventral corner of anterior adductor scar and connecting to antero-ventral corner of posterior adductor scar without pallial sinus.

**Measurements:** See Table 1.

**Holotype:** Right valve preserving its dentition and adductor muscle scars with pallial line on internal mold, SFMCM-0182 (Figures 11 and 12).

**Paratypes:** One left valve with its dentition preserved, SFMCM-0178 (Figures 8–10); four closed valves partly





**Figures 8–23.** *Pliocardia?* *tanakai* new species. All specimens are from Loc. 1. **8–10.** Lateral (**8**) and dorsal (**9**) views, and hinge (**10**) of left valve; Paratype, SFMCM-0178. White arrow shows lumular incision. **11–12.** Right valve hinge (**11**) and inner mold of right valve (**12**); **aas**, anterior adductor muscle scar; Holotype, SFMCM-0182. White arrow shows lack of pallial sinus. **13–15.** Dorsal (**13**), left lateral (**14**) and right lateral (**15**) views; **aas**, anterior adductor muscle scar; **pas**, posterior adductor muscle scar; Paratype, SFMCM-0180. White arrows show lumular incision (**13**) and lack of pallial sinus (**14**). **16.** Right lateral view with inner mold in part; Paratype, SFMCM-0181. **17–18.** Left lateral view (**17**) and right lateral view with inner mold in part (**18**); Paratype, SFMCM-0183. **19–21.** Dorsal view (**19**), left lateral (**20**) and right lateral (**21**) views of inner mold; **aas**, anterior adductor muscle scar; **pas**, posterior adductor muscle scar; Paratype, SFMCM-0179. White arrow shows lack of pallial sinus. **22–23.** Right lateral (**22**) and left lateral (**23**) views of inner mold; SFMKT-00399. Scale bar = 10 mm (for all figures).

exhibiting internal molds with adductor scars and pallial lines, SFMCM-0180 (Figures 13–15), 0181 (Figure 16), 0183 (Figures 17 and 18), 0179 (Figures 19–21).

**Other Examined Material:** One inner mold of both valves, SFMCM-0184; three conjoined valves from

Loc. 1, which were once described by Tanaka (1959) as *Liocyra* cf. *terrera* (No. 520 in Tanaka, 1959, pl. III, figs. 21 and 22), registered now as SFMKT-00398, and *Paphia* sp. (No. 521 in Tanaka, 1959, pl. III, fig. 23), registered now as SFMKT-00399.



**Table 1.** Measurements of *Pliocardia?* *tanakai* new species from Loc. 1.

| Specimen number | Type     | Length (mm) | Height (mm) | Width (mm) | H/L  | W/L  | Valve |
|-----------------|----------|-------------|-------------|------------|------|------|-------|
| SFMCM-0178      | Paratype | 18.0+       | 13.2        | -          | -    | -    | left  |
| SFMCM-0179      | Paratype | 24.6        | 16.3        | 9.9        | 0.66 | 0.40 | both  |
| SFMCM-0180      | Paratype | 23.5        | 15.8        | 10.0       | 0.67 | 0.43 | both  |
| SFMCM-0181      | Paratype | 15.9        | 12.3        | 7.3        | 0.77 | 0.46 | both  |
| SFMCM-0182      | Holotype | 24.2+       | 16.2        | -          | -    | -    | right |
| SFMCM-0183      | Paratype | 10.2        | 8           | 5.6        | 0.78 | 0.55 | both  |
| SFMCM-0184      |          | 17.4        | 12.7        | 7.8        | 0.73 | 0.45 | both  |
| SFMKT-00398-1   |          | 18.9+       | 13.0        | 7.4        | -    | -    | both  |
| SFMKT-00398-2   |          | 20.8        | 12.0        | 5.8        | 0.57 | 0.28 | both  |
| SFMKT-00399     |          | 28.4        | 18.6        | 12.8       | 0.66 | 0.45 | both  |

**Type Locality:** Akanuda and Anazawa, Matsumoto City, Nagano Prefecture, central Japan (Loc. 1 in Figure 1).

**Distribution:** Only from the type locality, middle Miocene Bessho Formation in Nagano Prefecture, central Japan.

**Etymology:** Named after the Emeritus Professor Kumio Tanaka, who made great contributions to the geology and paleontology of Nagano Prefecture.

**Remarks:** The present species is tentatively assigned to the genus *Pliocardia* because of its ovate shell outline, a right valve hinge having stout ventral cardinal (1) and arched subumbonal cardinals (very short 3a and 3b), and a distinct lunular incision, which are the diagnostic characters of the genus *Pliocardia* as redefined by Krylova and Janssen (2006). However, this species lacks the following two diagnostic characters: 1) a shallow pallial sinus and 2) a radial depression on the external shell surface running from the umbo to the postero-ventral margin. Considering that the genus *Pliocardia* is taxonomically uncertain at present as mentioned by Martin and Goffredi (2012), we avoid at this point erection of a new genus for this species.

This species is also similar to the species of *Waisiuconcha* Beets, 1942, in its ovate or subcircular shell outline, strong ventral cardinal (1) and arched subumbonal cardinals (3a and 3b) in the right valve hinge, well-defined lunular incision, and lacking of a pallial sinus (Cosel and Salas, 2001). *Waisiuconcha* has, however, a pallial line distant from the ventral margin, while the present species has a pallial line close to the ventral margin. Moreover, *Waisiuconcha* also lacks a radial depression or an inner ridge on the shell surface.

*Pliocardia?* *tanakai* new species resembles the type species of the genus *Austrogena* Krylova, Sellanes, Valdés, and D'Elia, 2014, which was recently described from the Chilean margin, in the presence of a lunule and an escutcheon, its hinge dentitions of both valves, and the absence of a pallial sinus. The genus *Austrogena*, however, has an oval to more rectangular shell and a less impressed lunular incision than *P.?* *tanakai*. Moreover, the hinge plate of adult *Austrogena* is characterized by the presence of a subumbonal pit, which is absent in

*P.?* *tanakai*. *Austrogena* is known only from the southeastern Pacific at present (Krylova et al., 2014).

The genus *Notocalyptogena* Amano, Saether, Little, and Campbell, 2014 also has a radial internal ridge similarly to *Pliocardia?* *tanakai*. However, *Notocalyptogena* can be clearly distinguished from the present species by its larger, elongate shell, a longer anterior cardinal tooth (3a) in the right valve, and lacking a lunule.

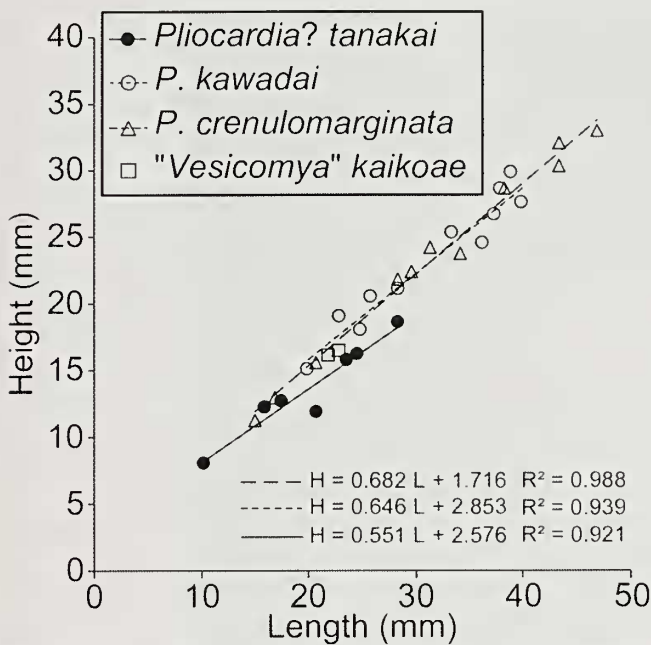
*Pliocardia?* *tanakai* is the second Japanese fossil species assignable to this genus. *Pliocardia kawadai* (Aoki, 1954) has been known as the only Japanese fossil species of this genus, and it has been reported from the lower to middle Miocene seep and whale-fall sites in the central to northern Japan (Amano and Kiel, 2012).

**Comparisons:** *Pliocardia?* *tanakai* new species can be clearly distinguished from the other two Japanese *Pliocardia* species, i.e., *P. kawadai* from the lower to middle Miocene and the living species *P. crenulomarginata* (Okutani, Kojima and Iwasaki, 2002), by having a smaller and lower shell (Figure 24) and by lacking a pallial sinus and a distinct radial depression from the beak to the postero-ventral corner on the external shell surface.

*Pliocardia?* *tanakai* resembles *Pliocardia?* sp. from the upper Oligocene part of the Lincoln Creek Formation in western Washington State, USA (Amano and Kiel, 2007, 2012) in shell size and outline, but differs from it in lacking a depressed area running from the beak to the posterior corner on the external shell surface and in having a weaker anterior cardinal tooth (3a) in the right valve.

Amano and Kiel (2012) suggested that some of the Paleogene vesicomid species from the North Pacific realm which were previously assigned to *Archivesica*, including the oldest known vesicomid “*Archivesica*” cf. *tchudi* (Olsson, 1931) from the upper middle Eocene Humpulips Formation in western Washington, USA, may belong to *Pliocardia*. *Pliocardia?* *tanakai* resembles “A”. cf. *tchudi* illustrated in Amano and Kiel (2007) in having an ovate shell outline, an inner ridge just before the posterior adductor muscle scar, and no pallial sinus, but is distinct from the latter by a more posteriorly situated beak, a non-undulated anterior cardinal tooth (2a), and lacking of a subumbonal pit. *P.?* *tanakai* is also similar to *Vesicomya* aff. *tchudi* Olsson, 1931 reported





**Figure 24.** Relationships between shell length and height with growth of *Pliocardia?* *tanakai* new species, *P. kawadai* (Aoki), *P. crenulomarginata* (Okutani, Kojima and Iwasaki), and “*Vesicomya*” *kaikoeae* Okutani, Fujikura and Kojima. Measurements of *P. kawadai* are from Kamada (1962) and Amano et al. (2001), those of *P. crenulomarginata* are from Krylova and Janssen (2006), and those of “*V.* *kaikoeae* are from Okutani et al. (2000).

by Squires and Gring (1996) from the upper Eocene Wagonwheel Formation in California, USA, in its shell size and shape. Although the specimens of Squires and Gring (1996) did not show the hinge characters and seems to be somewhat deformed, they are clearly distinguishable from *P.?* *tanakai* by a truncated posterior end.

*Pliocardia?* *tanakai* also resembles *Pliocardia?* sp. from the lower to middle Miocene Bexhaven Limestone, New Zealand (Amano et al., 2014) in its shell outline with a subtruncated posterior margin, a lunular incision, and a blunt ridge running from the beak to the postero-ventral corner, but differs from the latter species in lacking a pallial sinus. Moreover, the posterior cardinal tooth (3b) of *P.?* *tanakai* is not as strong as that of *Pliocardia?* sp. from the Bexhaven Limestone.

Some specimens of *Calyptogena pacifica* Dall, 1891 from the upper Miocene in Japan (Amano and Jenkins, 2011) have an ovate shell outline like *Pliocardia?* *tanakai*. *Calyptogena pacifica* also has an escutcheon and lacks a pallial sinus, but can be distinguished from *P.?* *tanakai* by having a less inflated shell and lacking a lunule.

*Pliocardia?* *tanakai* resembles the Recent “*Vesicomya*” *kaikoeae* Okutani, Fujikura and Kojima, 2000 in shell size and outline (Figure 24), the presence of a lunular incision, and the right valve dentition having a ventral tooth (1) overlaid by arched cardinals (3a and 3b). But “*Vesicomya*” *kaikoeae* has a pallial line with a shallow

embayment which is absent in *P.?* *tanakai*. Recently, molecular phylogenetic analyses revealed that “*V.*” *kaikoeae* is well separated from the other vesicomimid species including *Pliocardia* species (Kojima et al., 2004; Krylova and Sahling, 2010; Decker et al., 2012).

### Genus *Adulomya* Kuroda, 1931

**Type Species:** *Adulomya uchimmraensis* Kuroda, 1931 from the middle Miocene Bessho Formation in central Honshu, Japan (monotypy).

**Remarks:** The genus *Adulomya* was redefined by Amano and Kiel (2007) and characterized by its elongate shell, two radiating cardinal teeth in the right valve hinge, and lacking of a pallial sinus except for *A. chitanti* Kanehara, 1937 (Amano and Kiel, 2011). *Adulomya* first appeared in the eastern Pacific in late Eocene age (Amano and Kiel, 2007) and invaded into Japan in the early Miocene (Amano and Kiel, 2011). Japanese *Adulomya* showed its high species diversity during early to middle Miocene in lower sublittoral to middle bathyal depths, but declined with replacement by other vesicomimid genera such as *Archivesica* and *Calyptogena* since the late Miocene (Amano and Kiel, 2011).

### *Adulomya akanudaensis* (Tanaka, 1959)

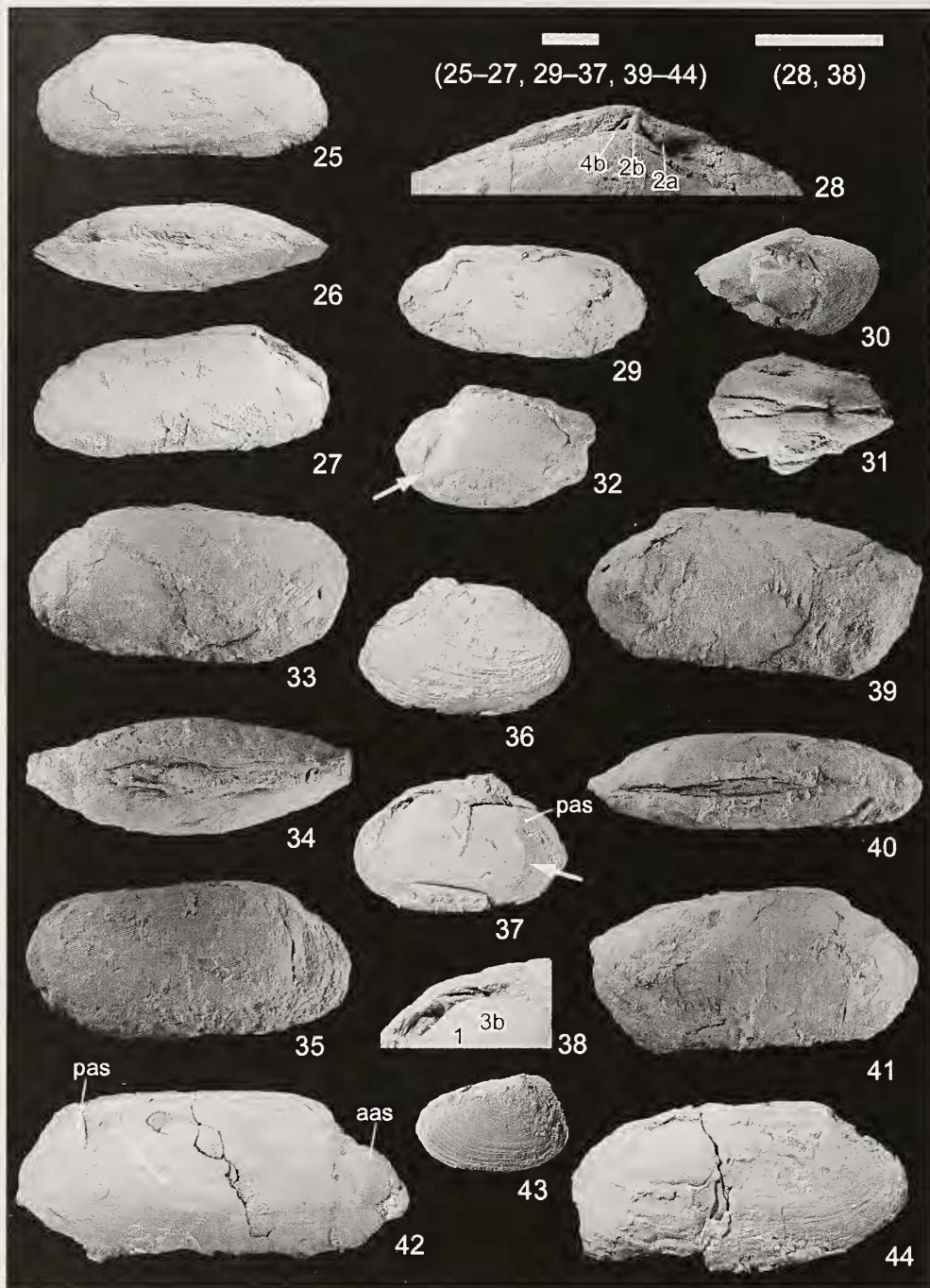
#### new combination

(Figures 25–44)

*Calyptogena akanudaensis* Tanaka, 1959: 119–120, pl. 2, figs. 1–9; Amano and Kiel, 2011: 84, figs. 27–29.

**Redescription:** Shell thin, moderate in size (up to 71.1 mm long), elongated elliptical in shape (height/length = 0.39–0.68), equivalve and inequilateral, slightly to moderately inflated (width/length = 0.24–0.40), sculptured by fine commarginal growth lines with wider interspaces in posterior part. Antero-dorsal margin nearly straight to slightly concave, graduating to rounded or slightly protruded anterior margin; postero-dorsal margin nearly straight and parallel to ventral margin or slightly convex, continuing to rounded posterior margin; ventral margin straight, broadly arcuate in juvenile (length < 27 mm), or slightly concave at its central part in some specimens. Beak low, prosogyrate, and situated at 16–40% of shell length from anterior margin. Lunule and escutcheon absent. Right valve hinge: anterior cardinal tooth (3a) reduced; central cardinal tooth (1) small, triangular, situated below umbo, with hollow space between its dorsal end and umbo; posterior cardinal tooth (3b) moderately thick, bifid, subparallel to postero-dorsal shell margin, detached from central cardinal tooth (1). Left valve hinge: anterior cardinal tooth (2a) thick, oblique anteriorly, connecting with central cardinal tooth (2b) in their proximal parts at acute angle; central cardinal tooth (2b) stout, situated just below umbo, tapered to proximal part, nearly perpendicular to hinge base; posterior cardinal tooth (4b) thin, weak, oblique posteriorly, connecting with central cardinal tooth (2b) as with





**Figures 25–44.** *Adulomya akanudaensis* (Tanaka). Specimens of Figures 25–35 and 39–41 are from Loc. 1 (type locality) and those of Figures 36–38 and 42–44 are from Loc. 3. **25–28.** Left lateral view (25), dorsal view (26), and right lateral view of inner mold (27), and left valve hinge (28); Neotype, SFMKT-00404. **29.** Left lateral view with inner mold; Paratype, SFMKT-00401. **30–31.** Right lateral view of a small specimen, SFMKT-00405-1 (paratype), attached on a large specimen, SFMKT-00405-2 (30), and dorsal view of a large specimen, SFMKT-00405-2 (31). **32.** Left lateral view with inner mold; Paratype, SFMKT-00406. White arrow shows inner rib. **33–35.** Left lateral (33), dorsal (34), and right lateral (35) views; Paratype, SFMKT-00403. **36–38.** Right lateral view (36), left lateral view of inner mold (37), and right valve hinge (38); pas, posterior adductor muscle scar; SFMCM-0191. White arrow shows lack of pallial sinus. **39–41.** Left lateral view of inner mold (39), dorsal view (40), and right lateral view of inner mold (41); Paratype, SFMKT-00402. **42.** Right lateral view of inner mold; aas, anterior adductor muscle scar; pas, posterior adductor muscle scar; SFMCM-0185. White arrow shows inner ridge. **43.** Right lateral view; SFMCM-0189. **44.** Right lateral view; SFMCM-0188. Scale bars = 10 mm (for all figures).



anterior cardinal tooth (2a). Anterior adductor muscle scar well impressed and ovate, with a distinct inner rib running from beak to base of posterior margin of anterior adductor scar. Posterior adductor muscle scar ovate and indistinct except for its anterior margin, with a blunt inner ridge running from postero-dorsal shell margin to antero-ventral corner of posterior adductor scar. Pallial line indistinct in ventral part, starting at postero-ventral corner of anterior adductor scar and connecting with antero-ventral corner of posterior adductor scar without pallial sinus.

**Measurements:** See Table 2.

**Type Material:** The holotype was originally designated and illustrated by Tanaka (1959, pl. II, figs. 5 and 6, a specimen “No. 510”). Specimens SFMKT-00389 in the Kunio Tanaka’s collection at the Shinshushinmachi Fossil Museum are with an original label “No. 510”, but

all of the specimens are clearly different from the illustrated holotype. Moreover, we could not find any specimens corresponding to the holotype illustration in the collection. We therefore judge that the holotype is lost and designate a neotype as a conjoined valve preserving the left hinge dentition (Figures 25–28), SFMKT-00404 (No. 527 in Tanaka, 1959, one of his paratypes); six paratypes excluding SFMKT-00404 designated in Tanaka (1959), i.e., SFMKT-00144 (No. 255 in Tanaka, 1959, pl. II, figs. 1–4), SFMKT-00401 (No. 524, pl. II, fig. 8), SFMKT-00402 (No. 525, pl. II, fig. 9), SFMKT-00403 (No. 526, pl. II, fig. 7), SFMKT-00405 (No. 528), SFMKT-00406 (No. 529), and SFMKT-00407 (No. 530). Tanaka (1959) also designated No. 531 (SFMKT-00408) as a paratype, but it was identified as another species, *Adulomya uchimuraensis*.

**Type Locality:** Akanuda, Matsumoto City, Nagano Prefecture, central Japan (Loc. 1 in Figure 1).

**Table 2.** Measurements of *Adulomya akanudaensis* (Tanaka) from Loc. 1 and 3.

| Specimen number | Type     | Length (mm) | Height (mm) | Width (mm) | H/L  | W/L  | Valve | Loc. |
|-----------------|----------|-------------|-------------|------------|------|------|-------|------|
| SFMKT-00144     | Paratype | 54.4+       | 26.8        | -          | -    | -    | right | 1    |
| SFMKT-00401     | Paratype | 42.3        | 18.8        | -          | 0.44 | -    | both  | 1    |
| SFMKT-00402     | Paratype | 57.4+       | 27.7        | 16.1+      | -    | -    | both  | 1    |
| SFMKT-00403     | Paratype | 55.6        | 27.7        | 19.9+      | 0.50 | -    | both  | 1    |
| SFMKT-00404     | Neotype  | 51.1        | 21.6        | 14.9       | 0.42 | 0.29 | both  | 1    |
| SFMKT-00405-1   | Paratype | 9.6+        | 5.5         | -          | -    | -    | both  | 1    |
| SFMKT-00405-2   |          | 32.1+       | 21.1+       | -          | -    | -    | both  | 1    |
| SFMKT-00406     | Paratype | 34.6+       | 22.1        | 15.3       | -    | -    | both  | 1    |
| SFMCM-0185      |          | 67.9        | 29.8        | 22.1       | 0.44 | 0.33 | both  | 3    |
| SFMCM-0186      |          | 45.7        | 19.8        | 11.0       | 0.43 | 0.24 | both  | 3    |
| SFMCM-0187      |          | 51.4        | 21.9        | -          | 0.43 | -    | right | 3    |
| SFMCM-0188      |          | 59.8        | 29.3        | 17.5       | 0.49 | 0.29 | both  | 3    |
| SFMCM-0189      |          | 27.4        | 17.0        | 9.2        | 0.62 | 0.34 | both  | 3    |
| SFMCM-0190      |          | 65.5        | 34.3        | -          | 0.52 | -    | both  | 3    |
| SFMCM-0191      |          | 38.1        | 23.4        | 15.1       | 0.61 | 0.40 | both  | 3    |
| SFMKT-07227     |          | 38.8+       | 20.4        | 11.9       | -    | -    | both  | 3    |
| SFMKT-07228-1   |          | 22.1        | 12.9        | 7.9        | 0.58 | 0.36 | both  | 3    |
| SFMKT-07228-2   |          | 24.6        | 14.8        | 7.1        | 0.60 | 0.29 | both  | 3    |
| SFMKT-07228-3   |          | 10.0        | 6.8         | -          | 0.68 | -    | right | 3    |
| SFMKT-07229-1   |          | 23.7        | 14.3        | 7.9        | 0.60 | 0.33 | both  | 3    |
| SFMKT-07229-2   |          | 20.6+       | 12.4        | 8.1        | -    | -    | both  | 3    |
| SFMKT-07229-3   |          | 20.7+       | 12.2        | 6.7        | -    | -    | both  | 3    |
| SFMKT-07230-1   |          | 56.0        | 21.7        | 15.3       | 0.39 | 0.27 | both  | 3    |
| SFMKT-07230-2   |          | 31.2+       | 17.9        | -          | -    | -    | right | 3    |
| SFMKT-07230-3   |          | 41.4+       | 21.0        | -          | -    | -    | left  | 3    |
| SFMCM-0156      |          | 63.2        | 29.0        | -          | 0.46 | -    | both  | 3    |
| SFMCM-0157      |          | 38.9        | 16.3        | 10.5       | 0.42 | 0.27 | both  | 3    |
| SFMCM-0158      |          | 37.1        | 17.1        | 10.4       | 0.46 | 0.28 | both  | 3    |
| SFMCM-0162      |          | 29.3        | 13.4        | 7.5        | 0.46 | 0.26 | both  | 3    |
| SFMCM-0164      |          | 53.1        | 25.0        | 20.3       | 0.47 | 0.38 | both  | 3    |
| SFMCM-0165      |          | 65.7        | 29.7        | 22.6       | 0.45 | 0.34 | both  | 3    |
| SFMCM-0166      |          | 53.2        | 23.0        | 16.5       | 0.43 | 0.31 | both  | 3    |
| SFMCM-0167      |          | 66.1        | 29.6        | -          | 0.45 | -    | both  | 3    |
| SFMCM-0168      |          | 63.6        | 29.0        | -          | 0.46 | -    | left  | 3    |
| SFMCM-0169      |          | 71.1        | 32.9        | 25.1       | 0.46 | 0.35 | both  | 3    |
| SFMCM-0170      |          | 46.9        | 22.5        | 15.0       | 0.48 | 0.32 | both  | 3    |
| SFMCM-0171      |          | 28.5        | 15.0        | 9.4        | 0.53 | 0.33 | both  | 3    |

**Other Examined Material:** In addition to type materials from Loc. 1 (SFMKT-00401 to 00407), more than fifty specimens were collected from Loc. 3 and twenty-nine well-preserved specimens of them were measured and examined, SFMCM-0185 to 0191, SFMKT-07227 to 07230, SFMCM-0156 to 0158, 0162, and 0164 to 0171.

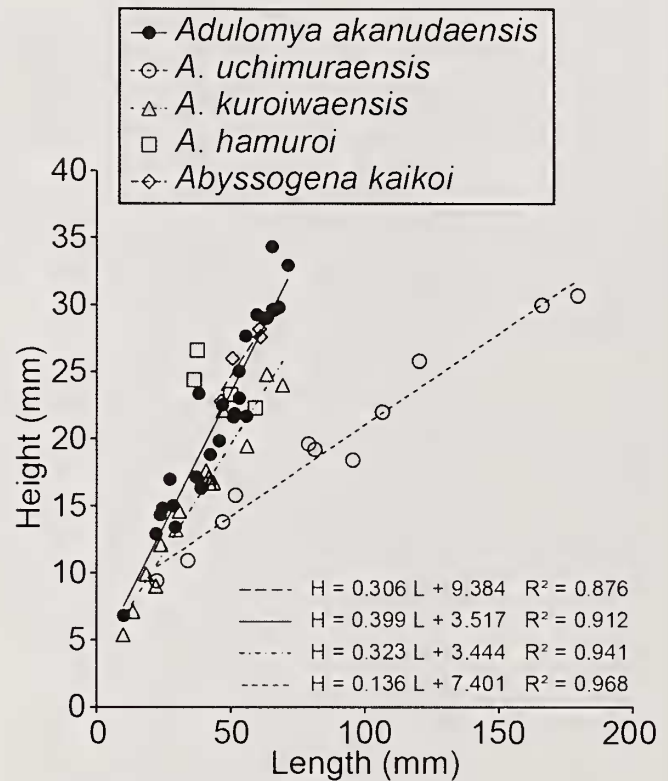
**Remarks:** This species was originally described by Tanaka (1959) as *Calyptogena akanudaensis*, which is distinct from the sympatric vesicomyid *Adulomya uchimuraensis* by its less elongated shell outline. The generic assignment of this species has been pointed out to be problematic because its internal shell characters were unknown (Amano and Kiel, 2011). We reexamined the paratypes and succeeded in exposing the left valve hinge consisting of three cardinals, 2a, 2b, and 4b (Figure 28). Moreover, we obtained many additional specimens from Loc. 3 and revealed that the right valve hinge is composed of two cardinals, 1 and 3b (Figure 38). These hinge dentitions agree well with those of *Adulomya*, and are inconsistent with an assignment to *Calyptogena* Dall, 1891, which has three cardinal teeth and a posterior nymphal ridge on the right valve.

The reassignment of this species from *Calyptogena* to *Adulomya* is consistent with the temporal distribution of other vesicomyid species around the Japanese islands, which was reviewed by Amano and Kiel (2007, 2011), Amano and Jenkins (2011), and Amano (2014). According to them, *Adulomya* diversified in the middle Miocene in both the Pacific and the Japan Sea sides, whereas *Calyptogena* first appeared in the late Miocene in the Japan Sea borderland.

**Comparisons:** It can clearly be ruled out that *Adulomya akanudaensis* represents juvenile shells of *A. uchimuraensis*, because the former has a much higher shell than the latter (Figure 45). Moreover, juveniles of *A. akanudaensis* have ovate and more inflated shells with a less protruded anterior margin than the juveniles of *A. uchimuraensis*.

Smaller specimens of *Adulomya hamuroi* Amano and Kiel, 2011 from the uppermost lower or lowest middle Miocene in Toyama Prefecture, Japan are similar to *A. akanudaensis* in their elongated elliptical shells, but are different from *A. akanudaensis* by having a slightly higher shell with a concave ventral margin. Moreover, *A. akanudaensis* has a less stout central cardinal tooth (1) in the right valve than *A. hamuroi* and the central cardinal tooth (2b) in the left valve is not bifid as *A. hamuroi*.

Amano and Kiel (2011) pointed out that some specimens of *Adulomya akanudaensis* have similar proportions as *A. kuroiwaensis* Amano and Kiel, 2011 from the uppermost middle or lowest upper Miocene in Niigata Prefecture, Japan, but *A. kuroiwaensis* has a more anteriorly situated beak and an expanded posterior part. Based on the examined specimens of *A. akanudaensis* herein, this species has a higher shell than *A. kuroiwaensis* (Figure 45), and has a hollow space between the umbo



**Figure 45.** Relationships between shell length and height with growth of *Adulomya akanudaensis* (Tanaka) from Locs. 1 and 3, *A. uchimuraensis* Kuroda, *A. kuroiwaensis* Amano and Kiel, *A. hamuroi* Amano and Kiel, and *Abyssogena kaikoi* (Okutani and Métivier). Measurements of *A. uchimuraensis* are from Kanno et al. (1998), those of *A. kuroiwaensis* and *A. hamuroi* are from Amano and Kiel (2011), and those of *Ab. kaikoi* are from Krylova et al. (2010).

and the central cardinal tooth (1) of the right valve that is absent in *A. kuroiwaensis*.

*Adulomya akanudaensis* resembles *A. chinookensis* (Squires and Goedert, 1991) from the upper Eocene to lower Oligocene in western Washington, USA in general shell outline and having a blunt ridge extending posteroventrally from the umbo. *A. chinookensis* was originally described as *Calyptogena chinookensis*, but Amano and Kiel (2007) revealed its dentition and reassigned it into the genus *Adulomya*. *Adulomya akanudaensis* is different from *A. chinookensis* by having a less elongate shell and a hollow space between the central cardinal tooth (1) and the umbo in the right valve.

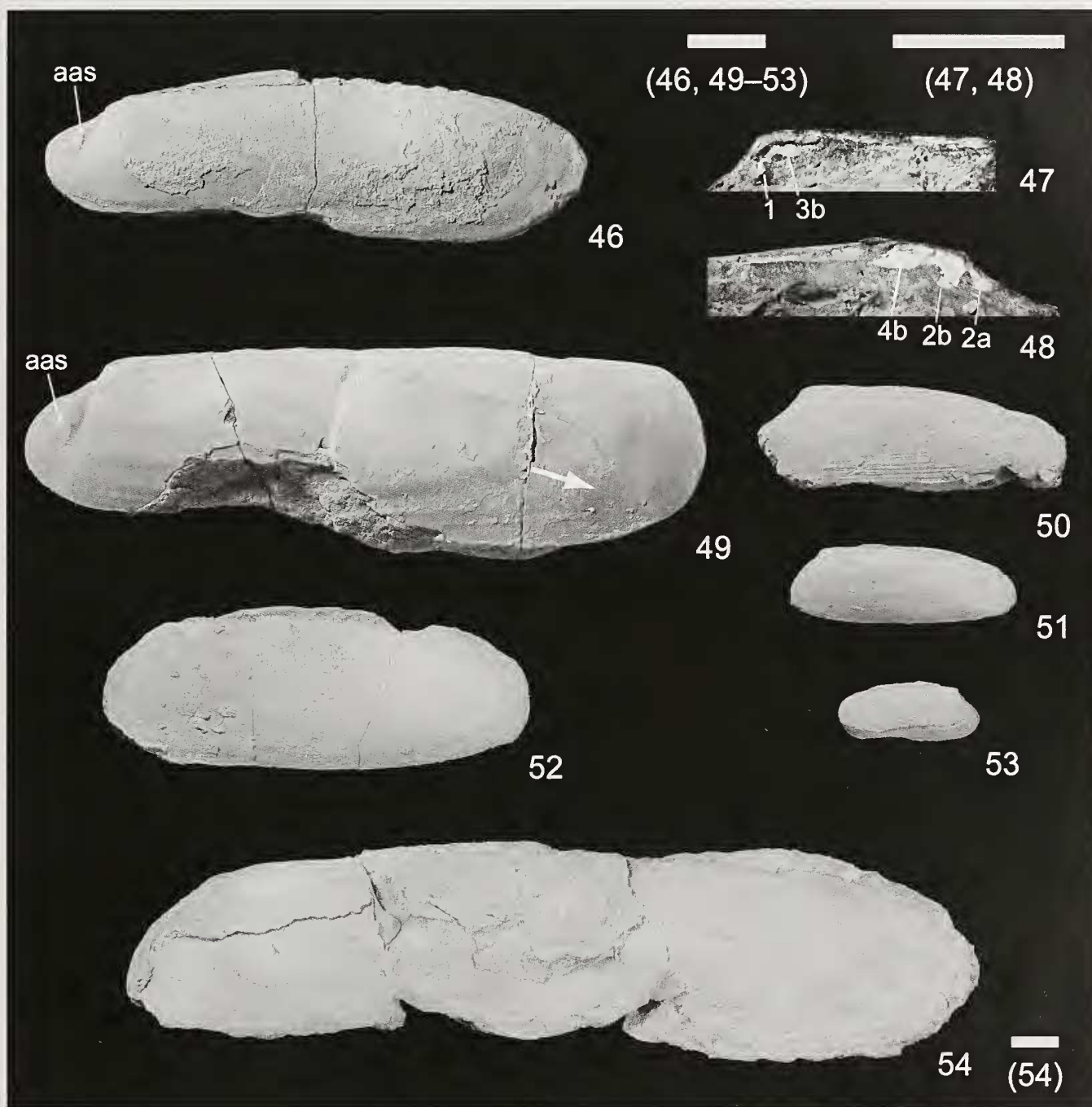
*Adulomya akanudaensis* is also similar to *Abyssogena kaikoi* (Okutani and Métivier, 1986) living in the Pacific side of Japan, in shell proportion (Figure 45) and non-fusing cardinals (1 and 3b) in the right valve. *Abyssogena kaikoi* was originally assigned to the subgenus *Ectenagena* Woodring (1938), which was later synonymized to the genus *Adulomya* by Amano and Kiel (2007). Krylova et al. (2010) established the new genus *Abyssogena* including *Abyssogena kaikoi* and stated that *Abyssogena*



differs from *Adulomya* by the absence of subumbonal pits and a pallial line originating from the ventral margin of the anterior adductor scar. *Adulomya akanudaensis* differs from *Abyssogena kaikoi* by lacking a pallial sinus and a bifid posterior cardinal tooth (3b) in the right valve.

**Distribution:** Middle Miocene Bessho Formation in Nagano Prefecture, Japan.

***Adulomya* sp. 1**  
(Figures 46–53)



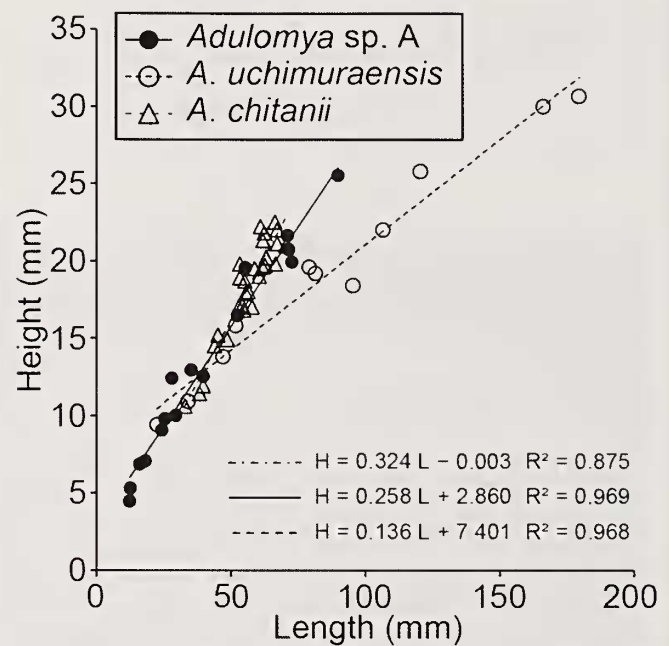
**Figures 46–53.** *Adulomya* species. 46–53. *Adulomya* sp. 1. All specimens are from Loc. 2. 46. Left lateral view of inner mold; aas, anterior adductor muscle scar; KUGSMM01. 47. Right valve hinge; KUGSMM78. 48. Left valve hinge; KUGSMM66. 49. Left lateral view of inner mold; aas, anterior adductor muscle scar; KUGSMM100-6. White arrow shows lack of pallial sinus. 50. Left lateral view; KUGSMM61. 51. Left lateral view of inner mold; KUGSMM103. 52. Left lateral view of inner mold; KUGSMM41. 53. Right lateral view of inner mold; KUGSMM84. 54. *Adulomya uchimuraensis* Kuroda from Loc. 1. Left lateral view with inner mold in part. Scale bars = 10 mm (for all figures).

**Description:** Shell small for genus (up to 89.9 mm long), elongate throughout ontogeny (height/length = 0.27–0.44), posteriorly expanded, equivalve and inequilateral, weakly inflated (width/length = 0.15–0.30), sculptured by fine growth lines widening in posterior part. Antero-dorsal margin nearly straight to broadly concave, gradually changing to narrowly rounded and slightly protruded anterior margin; postero-dorsal margin long and straight to broadly convex, continuing to rounded posterior margin gradually or a little abruptly at obtuse angle; ventral margin broadly arcuate or broadly concave in some specimens. Beak low, prosogyrate, situated at 7–21% of shell length from anterior margin. Lunule and escutcheon absent; ligament exterior, strong and long, occupying more than half of postero-dorsal margin. Right valve hinge: anterior cardinal tooth (3a) reduced; central cardinal tooth (1) thin, slightly oblique anteriorly from umbo; posterior cardinal tooth (3b) thick, oblique posteriorly. Left valve hinge: anterior tooth (2a) thick, subparallel to antero-dorsal shell margin, connected to central tooth (2b); central tooth (2b) as thick as anterior tooth (2a), vertical to hinge base; posterior tooth (4b) as thick as anterior (2a) and central (2b) teeth, connected to central tooth (2b), oblique posteriorly, but its distal end unknown. Anterior adductor muscle scar small and pear-shaped, with a distinct inner rib running from umbo to just below anterior adductor scar. Posterior adductor muscle scar indistinct. Pallial line only visible in posterior part, lacking pallial sinus. Indistinct radial interior striations visible in anterior part, running from umbo in slightly posterior direction.

**Measurements:** See Table 3.

**Material Examined:** Among one hundred and thirty collections from Loc. 2, sixteen entirely-preserved specimens were measured and examined, KUGSMM01, 08, 18, 41, 60, 61, 84, 92, 96, 99, 100, 101, and 103.

**Distribution:** Only from Sorimachi (Loc. 2), middle Miocene Bessho Formation in Nagano Prefecture, Japan.



**Figures 55.** Relationships between shell length and height with growth of *Adulomya* sp. 1 from Loc. 2, *A. uchimuraensis* Kuroda, and *A. chitanii* Kanehara. Measurements of *A. uchimuraensis* and *A. chitanii* are from Kanno et al. (1998) and Amano and Kiel (2011), respectively.

**Remarks:** The elongate shell and the hinge structures composed of two cardinals on the right and three cardinals on the left valve show that the vesicomysid fossils from Loc. 2 belong to the genus *Adulomya*. We tentatively describe them as *Adulomya* sp. 1 because of the poor preservation; most specimens are deformed and compressed inner molds or shells almost dissolved or replaced by sparry calcite, with the cardinal teeth unclear. *Adulomya* sp. 1 was previously reported as

**Table 3.** Measurements of *Adulomya* sp. 1 from Loc. 2.

| Specimen number | Length (mm) | Height (mm) | Width (mm) | H/L  | W/L  | Valve |
|-----------------|-------------|-------------|------------|------|------|-------|
| KUGSMM01        | 71.4        | 20.7        | 11.8       | 0.29 | 0.17 | both  |
| KUGSMM08        | 52.4        | 16.5        | 9.5        | 0.31 | 0.18 | both  |
| KUGSMM18        | 72.5        | 19.9        | 11.9       | 0.27 | 0.16 | both  |
| KUGSMM41        | 55.3        | 19.6        | 9.5        | 0.35 | 0.17 | both  |
| KUGSMM60        | 35.2        | 12.9        | 6.5        | 0.37 | 0.19 | both  |
| KUGSMM61        | 39.7        | 12.5        | 7.4        | 0.32 | 0.19 | both  |
| KUGSMM84        | 18.1        | 7.1         | -          | 0.39 | -    | both  |
| KUGSMM92        | 12.2        | 4.5         | 3.5        | 0.37 | 0.28 | both  |
| KUGSMM96        | 12.5        | 5.3         | 3.4        | 0.43 | 0.27 | both  |
| KUGSMM99        | 16.0        | 6.9         | -          | 0.43 | -    | both  |
| KUGSMM100-4     | 28.0        | 12.4        | 8.4        | 0.44 | 0.30 | both  |
| KUGSMM100-6     | 89.9        | 25.5        | 13.9       | 0.28 | 0.15 | both  |
| KUGSMM100-8     | 71.0        | 21.6        | -          | 0.30 | -    | both  |
| KUGSMM101-4     | 25.4        | 9.8         | 4.6        | 0.39 | 0.18 | both  |
| KUGSMM101-7     | 24.2        | 9.1         | 5.6        | 0.37 | 0.23 | both  |
| KUGSMM103       | 29.4        | 10.0        | 6.2        | 0.34 | 0.21 | both  |



*Adulomya uchimuraensis* (Tanaka, 1960; Seki, 1983; Miyajima et al., 2014), but is clearly distinguishable from *A. uchimuraensis* in having smaller and higher shells (Figures 54 and 55). *Adulomya* sp. 1 resembles *A. chitanii* Kanehara, 1937 in shell size and outline (Figure 55), but can be distinguished from *A. chitanii* by the lacking of a pallial sinus.

## DISCUSSION

Modern vesicomimid species diversity has been explained from the viewpoints of their bathymetric distribution (Fujikura et al., 2000), salinity or water temperature (Watanabe et al., 2013), and different preferences in hydrogen sulfide concentration at methane seeps (Barry et al., 1997; Sahling et al., 2002). On the other hand, little is known about the drivers of fossil vesicomimid species diversity. It is noteworthy that a total of four species, *Pliocardia?* *tanakai* new species, *Adulomya uchimuraensis*, *A. akanudaensis*, and *Adulomya* sp. 1, occur in a single formation. In particular, the former three species co-occur at the same seep carbonates, Akanuda and Anazawa limestones (Loc. 1). Such co-occurrence of more than two vesicomimid species seems to be rare in ancient seep environments. Although Kiel and Amano (2010) described three vesicomimid species, i.e., *Adulomya* sp. A, *Adulomya?* sp. B, and *Archivesica redwoodia* from a single site (USGS loc. 15399) in the lower Miocene Redwood Formation, Katalla District, southern Alaska, they are from a siliclastic sedimentary rock without seep carbonates.

Modern analogues of such co-occurrence of two or more species at a single seep site have been recognized in Sagami Bay (Kojima and Ohta, 1997) and Monterey Bay (Barry et al., 1997). In Sagami Bay, two sibling species, *Archivesica soyoae* and *A. okutanii* (reassigned to the genus *Phreagena* by Krylova and Sahling, 2010) have different preferences in salinity and temperature (Watanabe et al., 2013). In Monterey Bay, *Archivesica kilneri* (synonym of *soyoae*; Kojima et al., 2004; Okutani et al., 2009) and *Calyptogenia pacifica* have different physiological tolerances to hydrogen sulfide concentrations (Barry and Kochevar, 1998), and these two species are segregated along sulfide gradients from the center to the margin of the seeps (Barry et al., 1997).

In the Bessho Formation, such segregation of the vesicomimid species at seeps could not be recognized unequivocally. In the large-sized seep limestones (Loc. 1), *Adulomya uchimuraensis* is dominant and ubiquitous throughout the carbonate bodies and even in the neighboring siltstone. Autochthonous specimens of *Pliocardia?* *tanakai* were found by one of the authors (TN) in the peripheral part of the Anazawa limestone (Loc. 1), which also contains scattered shells of *A. uchimuraensis*. Although the mode of fossil occurrence of *A. akanudaensis* at Loc. 1 is unknown, *A. akanudaensis* may be mixed with *A. uchimuraensis* in local shell concentrations as in the small-sized carbonate body at Loc. 3.

It is noted that the relative abundances of the three vesicomimid species are different between Locs. 1 and 3. In the large-sized seep carbonate bodies at Loc. 1, *Adulomya uchimuraensis* dominates throughout the carbonates (more than 200 specimens have been collected), whereas *Pliocardia?* *tanakai* (only total 10 specimens were obtained by K. Tanaka and the authors) and *A. akanudaensis* (only 9 specimens were collected by K. Tanaka) are rare. In the small-sized carbonate body at Loc. 3, *A. akanudaensis* (more than 30 specimens were collected by the authors) is as abundant as *A. uchimuraensis*, but *P.?* *tanakai* could not be found. The sizes of seep deposits are often related to longevity of fluid-flow history or fluid flux (Luff and Wallmann, 2003; Luff et al., 2004; Nesbitt et al., 2013), and the larger carbonate size at Loc. 1 suggests a longer fluid-flow history or a higher fluid flux than Loc. 3. This is also supported by the difference in the associated other molluscan fossils between these localities. While the seep carbonates at Loc. 1 contain diverse molluscan fossils including bathymodioline mussels, which are known from high-flux seeps (e.g., MacDonald et al., 1989; Olu et al., 1996), the carbonate at Loc. 3 contains less diverse mollusks. Moreover, the lithology and carbon isotopic compositions of the carbonates are also different between Locs. 1 and 3. The large seep carbonates at Loc. 1 consist of muddy micrite and calcite veins, showing low  $\delta^{13}\text{C}$  values ( $-40$  to  $-36\%$ ; Sato et al., 1993), whereas the smaller carbonate body at Loc. 3 consists monotonously of micrite with  $\delta^{13}\text{C}$  values ranging from  $-29.8$  to  $+10.5\%$ . These suggest that the fluid intensity and composition, as well as longevity or flux, were different between the two seep sites (Peckmann et al., 2009; Kiel et al., 2014). Namely, an abundance of  $^{13}\text{C}$ -depleted void-filling cements, such as sparitic veins in the carbonates at Loc. 1, is often attributed to a vigorous, advective flow, whereas the absence of such early-diagenetic cements suggests diffusive seepage (Peckmann et al., 2009; Kiel et al., 2014). The carbon isotopic compositions of seep carbonates are thought to vary depending on fluid composition such as thermogenic or biogenic methane (Whiticar, 1999) or crude oil (Roberts and Aharon, 1994), or on fluid flux. Therefore, different preferences in these factors relating to the seep activity may have been related to the relative abundance of the three vesicomimid species in the Bessho Formation.

Fluid flux probably also played a role in controlling the distribution of *Adulomya* sp. 1. This species is restricted to Loc. 2, where several cm-sized small carbonate concretions, having  $\delta^{13}\text{C}$  values as low as  $-35\%$ , are scattered throughout the siltstone. Although the detailed study of this locality including carbon isotopic compositions of carbonates will be reported elsewhere, the scattered occurrence of small carbonate bodies suggests that the seepage was diffusive, with ephemeral and weak fluid flow (Nesbitt et al., 2013). In contrast, the larger seep carbonate bodies at Loc. 1 suggest longer fluid-flow history and a higher flow rate. The size difference between the seep deposits of Locs. 2 and 3 also suggests

some variation of seep activity, but it cannot be confirmed because most parts of the carbonate body at Loc. 3 originated from methanogenesis as well as methane oxidation.

In summary, the four fossil vesicomid bivalves in the middle Miocene Bessho Formation may have had different preferences for fluid flux rates, fluid composition, and longevities among seep sites. The vesicomid species diversity in this formation suggests that the diversification of vesicomids through the Cenozoic could have been sustained not only by geographic and bathymetrical separation but also by adaptation to various seepage conditions.

#### ACKNOWLEDGMENTS

We are grateful to Yumiko Watanabe (Kyoto University, Japan) for help in analyzing carbon and oxygen isotopic compositions of carbonate samples. We sincerely appreciate valuable comments and critical reviews by Steffen Kiel (Swedish Museum of Natural History, Stockholm), Elena M. Krylova (Russian Academy of Sciences, Russia), and the editor José H. Leal (Bailey-Matthews National Shell Museum, USA), which help improve our manuscript. Financial support was provided by JSPS KAKENHI (18340165 and 23540548 to TN: Grant-in-Aid for Scientific Research by Japan Society for Promotion of Science).

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